

# The Biology of the Northeastern Pacific Turridae. III. The Habitat and Diet of *Kurtziella plumbea* (Hinds, 1843)

by

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*Abstract.* The habitat, diet, and some reproductive and mortality factors were determined for *Kurtziella plumbea*, a shallow-water turrid gastropod from the Puget Sound region. In a shallow subtidal area with four depth-related habitats, it was found more often in upper habitats, although all of the habitats available were sandy and had similar sedimentary characteristics. In a deeper area, it was found primarily in areas of silty mud. *Kurtziella plumbea* is a predator of polychaetes. At the shallow site, it specialized on the oweniid *Owenia fusiformis* and spionids. In the deeper area, it was more generalized, but the cirratulid *Tharyx multifilis* was the most abundant prey item.

Egg capsule deposition occurred in the spring. There were no nurse eggs, and the time until veligers left the capsule was about 18–20 days. Settlement and metamorphosis were not observed. Growth rates of 1 to 2 mm/yr for median-sized individuals, and 3 to 4 mm/yr for small individuals were indicated.

Potential predators may include crabs and fish, but mortality factors were not conclusively determined.

## INTRODUCTION

THE MOST WIDELY distributed turrid gastropod in the shallow northeastern Pacific is *Kurtziella plumbea* (Figure 1), which is found from Mazatlán (McLEAN in KEEN, 1971) to southcentral Alaska (Shimek, unpublished data). I examined two populations of *Kurtziella plumbea* (hereafter as *Kurtziella*) to determine habitat, dietary requirements, and aspects of predatory and reproductive behavior. I attempted to determine some of the reasons why this particular snail is so widespread. Two mutually contradictory statements about this species were examined. (1) The species is generalized in both its use of habitats and prey, and thus it can be found in many habitats. In effect, it would be a successful "Jack-of-all-trades." (2) The species is specialized in habitat and/or diet, but the array of suitable habitats is widespread, thus permitting the snail to be widespread. Several major questions were addressed. (1) What is the relationship of diet to the potential dietary resources present? (2) Are these animals dietary or habitat

specialists or generalists? (3) What is the effect of these predators upon their prey populations? (4) Are there any particular traits that limit their choices of habitats or prey?

## MATERIALS AND METHODS

### Study Sites

All sites were subtidal, since *Kurtziella* is rarely intertidal in this region. Two major study sites were chosen: Windy Point in Dyes Inlet in lower Puget Sound and off the University of Washington Friday Harbor Laboratories dock on San Juan Island (Figure 2). Additional specimens were collected from many other localities, particularly in the San Juan Islands (SHIMEK, 1977); however, at these latter sites I collected only distributional data; quantitative data were seldom obtainable. Distributional information was gathered by dredge or bottom tow. All quantitative field work was done using SCUBA.

The Windy Point area, WP (47°37'25"N, 122°40'30"W), ranges from -1.5 m to -9.0 m below MLLW. It is a topographically homogeneous, sandy subtidal region unbounded laterally and divisible into four visually distinctive habitats: upper bench, upper slope, lower slope,

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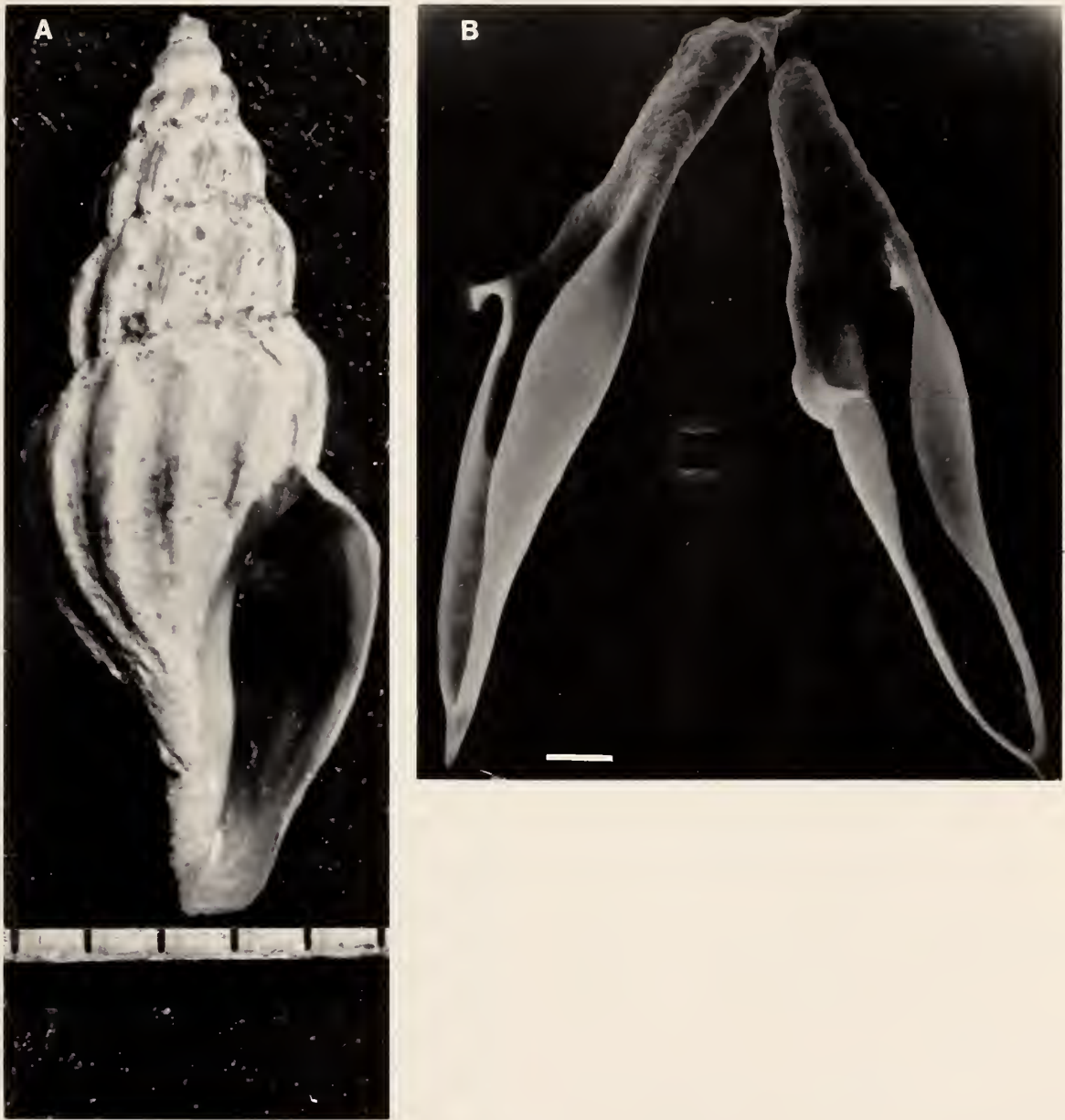


Figure 1

A. *Kurtziella plumbea* (Hinds, 1843). Scale in millimeters. B. Radular teeth of *Kurtziella plumbea*. Scale bar = 10  $\mu\text{m}$ . These are stabbing toxoglossan teeth used individually to pierce the prey and to introduce venom.

and lower bench, based upon the degree of slope, depth, and algal cover (SHIMEK, 1982). *Kurtziella* is found there with two other turrids, *Ophiidermella inermis* (Hinds, 1843) and *Oenopota levidensis* (Carpenter, 1864).

The Friday Harbor Laboratories site, FHL (48° 32'38"N, 123°00'50"W), is topographically diverse, containing five visually distinctive habitats: wood chips, rock, shell fragments, and shallow and deep areas of silty mud.

The site is located from -10 m to -25 m below MLLW. No discontinuities limit the site except at the upper edge where the boundary is established by the lower edge of an eelgrass, *Zostera marina* L., 1753, bed. No turrids were found in either the eelgrass or wood-chip areas in preliminary observations, consequently no quantitative sampling was done in either habitat. The remaining habitats were sampled quantitatively.

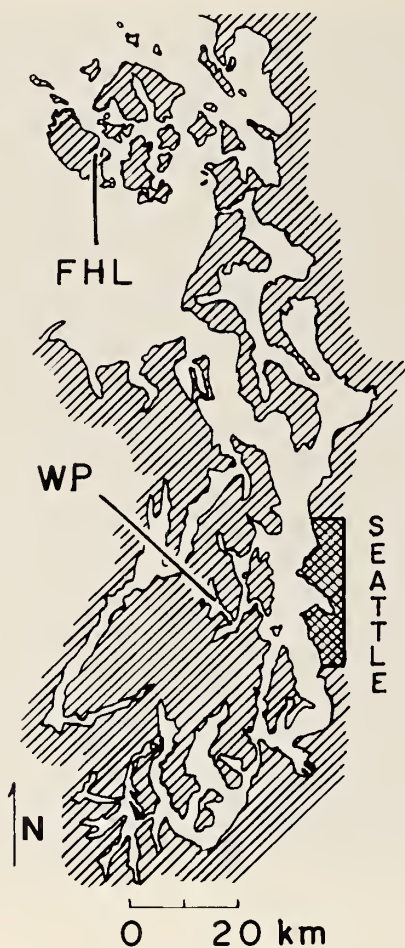


Figure 2

The Puget Sound region of Washington state showing the study sites.

### Habitat Analyses

At the major sites, the physical and biological properties of the habitats were examined in detail. Sediment particle-size distributions were quantitatively determined and the remainder of the sample was washed through a 0.5-mm sieve. The animals were removed and sorted by taxon. Gastropods and polychaetes were identified to species whenever possible. Other taxa were identified to class and counted, but not detailed further (see SHIMEK, 1982, for a more complete description of sampling methods).

Sediment parameters were tabulated and statistically compared between and within the areas. Seasonal variability of the sediment particle distributions was insignificant, thus no seasonal comparisons were made (SHIMEK, 1982).

Polychaete assemblage abundances for each habitat were determined by the quantitative, infaunal sampling, and

statistical comparisons were made between and within habitats on a seasonal basis (SHIMEK, 1982).

### Turrid Distribution, Collection, and Processing

Periodic transect studies from November, 1973, until December, 1975, were used to determine turrid distribution, seasonal or other distributional changes, and to provide a reference for the quantitative infaunal samples. The significance of *Kurtziella* distributions compared to random habitat utilizations were calculated using log-likelihood ratios (G-tests) (SOKAL & ROHLF, 1969).

A hand-held, semiquantitative dredge was used at FHL to determine the relative fraction of the turrid populations buried in the sediment. Simultaneous, parallel, surface-transect surveys were conducted to compare the number of snails buried and on the surface.

*Kurtziella* collected from FHL and WP were individually washed in sea water, isolated for up to a week, and feces were collected. The snail was then measured to the nearest 0.1 mm, and marked (SHIMEK, 1982). After marking, the animal was returned to fresh sea water at ambient sea-water temperature and observed to assure no noticeable effects of measuring and marking. The animal was then transferred to a "holding" aquarium and maintained in an artificial habitat similar to the normal one. All apparently healthy animals were returned to their habitat, albeit seldom to the point of capture, within two weeks. Measuring and marking mortality was about five percent.

Following marking and measuring, any particulate material remaining in the collecting jar was placed on a slide, dried, mounted in polyvinyl lactophenol (A. Kohn, personal communication), and examined microscopically. Identification of all fecal material was attempted. Feces consisted of mucus, radular teeth of the same animal, diatom frustules, and polychaete remains. Preliminary gut analysis by dissection indicated polychaetes swallowed whole to be the only prey. Thus only polychaete remains consisting of setae, jaws, and occasional cuticular strips were accepted as indicators of feeding. These remains were identified by comparison with descriptions, drawings, and setal preparations of known animals, identified with standard references (SHIMEK, 1982). Dietary heterogeneity was measured using  $H'$  (KOHN & NYBAKKEN, 1975). Turrids collected from other localities were preserved and their habitats noted, if the collecting was done with SCUBA, but no dietary analysis was attempted.

Size-frequency histograms were constructed for both populations. These were normalized to percent collected to facilitate comparison between populations because of varying sample sizes. For the purpose of determining growth rate, collections were considered quarterly: November through January as Winter; February through April as Spring; May through July as Summer; and August through October as Autumn. Generally these samples were too small and/or variable for quantitative determinations of recruitment cohorts (BLISS, 1967); however, I



attempted to use seasonal shifts in histogram peaks to estimate growth rates.

### Laboratory Experiments

A substrate-choice chamber was constructed, and filled to a depth of 2 cm with sediments (SHIMEK, 1982). The choices were sediments with a particle-size distribution from 0.250 to 0.500 mm, and a distribution in excess of 2.00 mm. Both sides had all detectable biota removed. Animals were placed in the chamber and one week later they were collected and their positions noted. These data were analyzed using cumulative binomial probabilities.

Egg capsules were collected from the jars in which the turrids were stored. Capsular dimensions were measured, the number of eggs per capsule was counted, and the egg diameters were measured (SHIMEK, 1982). The capsules were examined periodically. After hatching, the veligers were fed a mixture of *Isochrysis* sp. and *Dunaliella* sp.

## RESULTS

### Habitat Descriptions

**Windy Point:** The four Windy Point habitats have been described in detail elsewhere (SHIMEK, 1982). Briefly, these habitats were sandy, with moderately well-sorted, unconsolidated sediments. They were similar to each other and to the nearby sandy low intertidal areas. Algal cover in the shallower (depth < -5 m) areas varied seasonally, being very abundant in the late summer, and was mostly ulvoid algae. In the deeper areas the algal cover consisted of various red and brown algae and was less variable or dense.

**Friday Harbor Laboratories:** The FHL habitats are also described in SHIMEK (1982). Of the four major turrid habitats, only the rock areas could not be sampled quantitatively for infauna and sediment. Of the three unconsolidated-sediment areas, only the lower mud was physically different, having a distinctly smaller median-sediment-particle size.

### Biology of *Kurtziella* at Windy Point

*Kurtziella* was associated with the turrids *Ophiidermella inermis* and *Oenopota levidensis* at WP. All three were distributed in patches, and because of this, the mobility of these animals, and the lack of physical boundaries to the study area, no adequate estimates of population sizes could be made. Capture and transect observational frequencies did, however, give an estimate of relative population sizes. I collected or observed 254 *Ophiidermella inermis*, 134 *Kurtziella*, and 108 *Oenopota levidensis*. *Kurtziella* and *Oenopota levidensis* appeared to have roughly equivalent populations. During quantitative surveys, the density of *Kurtziella*, when found, varied from 0.01/m<sup>2</sup> to 0.16/m<sup>2</sup>. No seasonal trends in abundances or habitats utilized were seen, but *Kurtziella* was found more often in the shallower

Table 1

Windy Point *Kurtziella plumbea* habitat utilization.

Habitat	Proportion of total area	Proportion of turrids per area	Proportion of turrids observed - proportion expected
Upper bench	0.25	0.34	+0.09
Upper slope	0.25	0.26	+0.01
Lower slope	0.25	0.17	-0.08
Lower bench	0.25	0.24	-0.01
Number observed			134
Significance (G-test)	G = 9.40	P < 0.05	

areas at WP (Table 1). The sediment-particle distributions were not significantly different among most of these areas (SHIMEK, 1982). Depth was probably not a factor as *Kurtziella* was found in the deeper areas at FHL (Table 2).

There was a patchy distribution of the polychaete fauna at WP, particularly regarding the turrid prey species *Owenia fusiformis* delle Chiaje, 1844, which was dense only in the upper bench areas, and *Polydora socialis* (Schmarda, 1861), which was more widely distributed than *O. fusiformis* (Table 3). There was no seasonal pattern of predation at either site, consequently the prey-polychaete-abundance data were pooled. The high sample variability reflected seasonal abundance patterns for the worms; see

Table 2

Friday Harbor Laboratories *Kurtziella plumbea* habitat utilization.

Habitat	Proportion of total area	Proportion of turrids per area	Proportion of turrids observed - proportion expected
A. All habitats			
Upper mud	0.25	0.06	-0.18
Shell fragments	0.34	0.35	+0.01
Rock	0.05	0.06	+0.01
Lower mud	0.36	0.52	+0.16
Total number observed			48
Significance (G-test)			P < 0.01
B. Lower habitats only			
Shell fragments	0.45	0.38	-0.07
Rock	0.07	0.07	0.00
Lower mud	0.48	0.56	+0.08
Number observed			45
Significance (G-test)			n.s.

Table 3  
Density of prey species (mean number/m<sup>2</sup> ± 1 SD).

A. Area: Windy Point				
Habitats:	Upper bench	Upper slope	Lower slope	Lower bench
Prey species				
<i>Owenia fusiformis</i>	713 ± 413	197 ± 375	9 ± 22	0
<i>Polydora socialis</i>	843 ± 907	661 ± 591	468 ± 440	268 ± 440
<i>Spiophanes berkeleyorum</i>	0	0	5 ± 16	0
B. Area: Friday Harbor Laboratories				
Habitats:	Upper mud	Shell fragments	Lower mud	
Prey species				
<i>Myriochele oculata</i>	6 ± 19	0	0	
<i>Cirratulus cirratus</i>	31 ± 56	23 ± 37	20 ± 37	
<i>Tharyx multifilis</i>	136 ± 125	79 ± 77	157 ± 85	
<i>Spiophanes bombyx</i>		not sampled		

SHIMEK (1977, 1982) for more complete listings of the polychaetes.

*Kurtziella* was found to be widely, but unevenly, distributed in the Puget Sound region. I dredged and/or surveyed by SCUBA 40 different sites and *Kurtziella* was found in only six of them (SHIMEK, 1977). All six were characterized as sandy or sandy-mud habitats.

#### Dietary Analysis

Dietary information obtained by fecal examination is summarized in Table 4. *Kurtziella* at WP ate three species of identified polychaetes. Densities of the most common prey, *Owenia fusiformis*, fluctuated dramatically in all but the upper-bench area, and this worm was absent from the lower-bench area completely (Table 3).

#### Predation on *Kurtziella* at WP

In the WP-slope habitats predation by crabs upon the snails may have been an important factor. Two predatory

crabs were present, *Cancer gracilis* Dana, 1852, and *C. productus* Randall, 1839, although specimens of the latter were uncommon, probably because of too few suitable refuges (SHIMEK, 1982). During the summer when the crabs were common, *Kurtziella* became rare (Figure 3). Consequently, no laboratory verification of the attractiveness of *Kurtziella* as a prey item was attempted. *Cancer productus* will eat both *Oenopota levidensis* and the larger *Ophiidermella inermis* in the same area, and *Cancer gracilis* may eat small snails of all types. As *Kurtziella* was smaller than the other turrids at WP, it was a likely prey item for both crabs.

#### Biology of *Kurtziella* at Friday Harbor Laboratories

The turrid assemblage at FHL is diverse, in addition to *Kurtziella*, nine other turrids in three other genera are found there (SHIMEK, 1982, 1983). Habitat utilizations were determined from transect surveys. As with the other turrids at FHL, *Kurtziella* was less common in the upper-mud area than would be expected if it was randomly distributed (SHIMEK, 1982, 1983). If the upper-mud area is considered to be a boundary area that is incompletely utilized, and the data from this habitat are excluded, *Kurtziella* was collected most frequently in the lower-mud habitat (Table 2). When found, *Kurtziella* had measured abundances from 0.01/m<sup>2</sup> to 0.05/m<sup>2</sup>.

The polychaete fauna at FHL was diverse and sparse. The most abundant turrid prey, *Tharyx multifilis* (Moore, 1909), were present in most of the samples and habitats (Table 3). The infaunal assemblages from all of these habitats were similar in the summer, but in the winter the upper- and lower-mud areas had many differences (SHIMEK, 1982).

The substrate-preference experiments gave conclusive results, even with the small number of individuals available at any one time for each test. Of the animals tested,

Table 4

Results of fecal sample analysis of *Kurtziella plumbea*.

Area:	WP	FHL	Total
Prey species			
<i>Myriochele oculata</i>		1	1
<i>Owenia fusiformis</i>	13		13
<i>Polydora socialis</i>	1		1
<i>Spiophanes berkeleyorum</i>	2		2
<i>S. bombyx</i>		1	1
<i>Cirratulus cirratus</i>		1	1
<i>Tharyx multifilis</i>		3	3
Unidentified polychaetes	1	4	5
Number of snails examined	139	110	249
Percent feeding	12.2	9.1	10.8
H' (identified prey only)	0.60	1.24	1.36

17 animals made choices; 13 chose the sediment with smaller particle-size distribution (0.250 mm–0.500 mm), whereas only 4 chose the sediment with particles larger than 2.00 mm. The two-tailed binomial probability of a deviation this large or larger, given an equal probability of choice, is 0.049.

The hand-held, semiquantitative dredge was used infrequently as it resulted in substantial habitat damage. Data from these dredge samples indicated equivalent numbers of *Kurtziella* buried and on the surface at the times of the surveys. During the surface surveys, five *Kurtziella* were found in 583 m<sup>2</sup>. Simultaneous dredging parallel to, but 2 m lateral to the surface-survey-transect lines collected one *Kurtziella* in 116.6 m<sup>2</sup> dredged to a depth of 0.10 m.

### Dietary Analysis

Relatively few animals were found eating (Table 4), and no seasonal dietary trends were evident. At WP, *Kurtziella* was most often feeding on *Owenia fusiformis*, although sponiids were also found in the diet. At FHL, no such clear-cut pattern of specialization was evident, and the snails had a more catholic diet consisting of cirratulids, sponiids and oweniids. In contrast to the prey distribution at WP, the major prey taxon at FHL, the Cirratulidae, was common in all habitats (Table 3).

### *Kurtziella* Reproduction

Collection and confinement for fecal-sample examination acted as stimuli for egg-capsule deposition in some turrids (SHIMEK, 1982, 1983). Eight individuals of *Kurtziella* deposited egg capsules in captivity in March, April, and May, 1975 (Table 5). Single females deposited from one to three capsules. Capsules were smaller than the egg capsules of either *Oenopota* or *Ophiodermella*, and contained fewer, smaller eggs (SHIMEK, 1982, 1983). The egg capsules were deposited on the inside of the collection jar at the junction of the lateral and bottom surfaces. The eggs in 10 capsules hatched after about 18–20 days. As with *Oenopota* and *Ophiodermella*, there were no nurse eggs, and the number of veligers leaving the capsules was the same as the original number of eggs deposited. Four capsules contained eggs that did not develop at all. Presumably the stimulus for oviposition was so strong that unfertilized eggs were deposited in the capsules. These capsules appeared normal in all other respects. No egg capsules of *Kurtziella* were seen in the field.

### Life Histories

Seasonal size-frequency distributions can be examined for indications of growth rate, recruitment, and sizes of individuals in the population. A comparison of the FHL and WP populations yields some interesting observations. The WP population was composed of distinctly smaller individuals with virtually no animals exceeding 12 mm

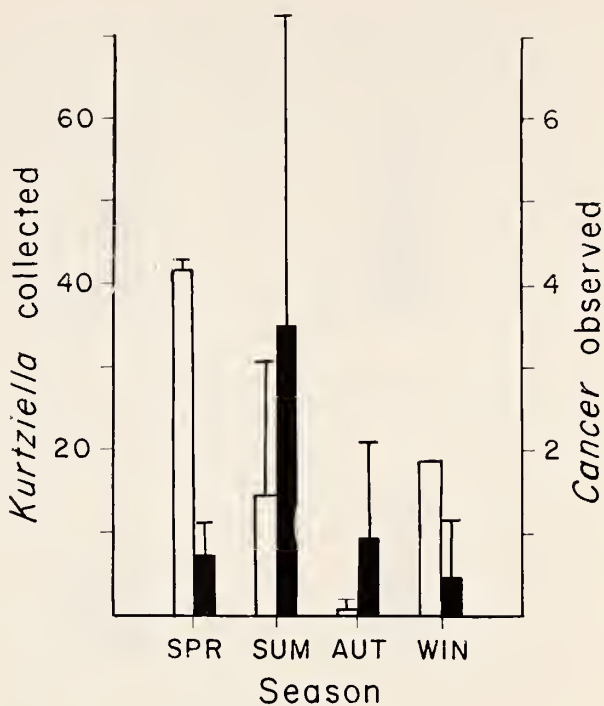


Figure 3

Mean ( $\pm 1$  SD) number of *Kurtziella plumbea* (open bars) collected and mean number of *Cancer gracilis* (black bars) observed (per 25 m<sup>2</sup>) by season. All habitats and seasons were pooled. Data are for Spring, 1974, through Autumn, 1975; therefore, *Kurtziella* was collected in only one winter.

total length (Figure 4). On the other hand, the FHL population was composed of larger animals, with almost no animals below 10 mm total length (Figure 5). Neither population showed appreciable seasonal shifts in the size-frequency histograms, although in both populations the mean individual length increased from spring to winter, and dropped again the following spring. The pattern of changes in the mean sizes in both distributions was virtually identical although consistently displaced by the amount the two populations differed in mean length. Examination of the seasonal shifts for both populations in-

Table 5

*Kurtziella plumbea* reproductive information.

	Mean capsule dimensions ( $\mu$ m)		Mean egg	
	Length	Width	Number/capsule	Diameter ( $\mu$ m)
	230 $\pm$ 34	186 $\pm$ 22	180 $\pm$ 43	137 $\pm$ 8
Number examined	13		6	9
Number of capsules hatching:	10			
Mean number of days in the capsule:	19.3 $\pm$ 1.16 days			
Maximum length of survival post hatching:	27 days			



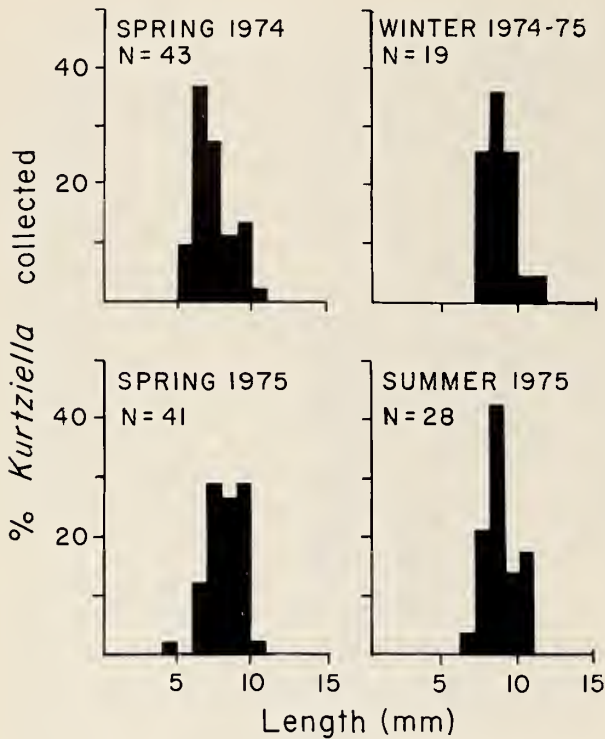


Figure 4

Windy Point seasonal size-frequency distributions. In seasons not shown (Summer, Autumn, 1974) too few snails were observed to make the data meaningful.

dedicated a growth rate, for a 7–8 mm-long individual, of about 1.5 mm/yr. No marked animals were recaptured from the WP population. Five previously marked individuals were recaptured from the FHL population. Three decreased in total length, and two increased. One of those two had grown 0.5 mm in 287 days, indicating a growth rate of less than 1 mm/yr. This individual was 11.9 mm long when initially captured, however; and the larger individuals may grow more slowly than smaller ones, which was a pattern seen in the other turrids examined from these areas (SHIMEK, 1982, 1983).

In both populations, distinctly smaller animals were recovered only in the spring. If this species has a faster growth rate in the smaller size classes, the 4–6 mm-long individuals recovered in the spring of one year may represent larvae settling the previous summer. Growth rate determinations were difficult for these animals due to their small size, the wide variation in lengths, and the lack of more than one clearly defined peak in the size-frequency histograms.

#### DISCUSSION

As with sympatric turrids in the genera *Oenopota* and *Ophiidermella*, *Kurtziella* eats tube-dwelling polychaetes;

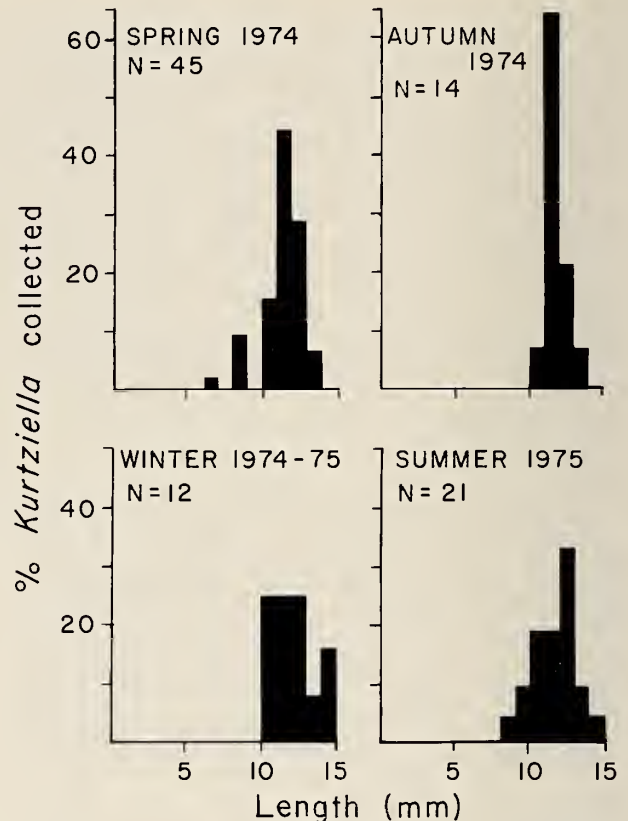


Figure 5

Friday Harbor Laboratories seasonal size-frequency distributions. In seasons not shown (Summer, 1974; Spring, 1975) too few snails were observed to make the data meaningful.

but the range of prey taken is quite broad, from oweniids to cirratulids, although at WP, *Owenia* predominates. The diversity of acceptable prey may be less at WP, possibly limiting animals in this population to fewer potential prey species. This might also explain the tendency of the *Kurtziella* to be found in areas where *Owenia* was common. Because manipulative experiments were not attempted, the turrid's effect on its prey is uncertain, but predation by *Kurtziella* alone probably did not have any substantial impact on the populations of its prey. The species appeared to have ample food sources; indeed, *Tharyx multifilis*, its major food, was one of the most abundant polychaetes in the FHL areas, and *Owenia fusiformis* was very abundant in some habitats at WP.

*Kurtziella* appears to be restricted to sandy or sandy-mud habitats and is rarely found on nearby rocky or shell-fragment habitats. Additionally, it seems to have substantial latitude in potential prey, although more data are needed to confirm this. The skewed distribution of *Kurtziella* at WP may indicate tracking of its most common prey species, *Owenia fusiformis*. *Owenia* was rarely found

below the upper-slope areas, and *Kurtziella* is more common in these upper areas than in the lower ones.

Predatory effects on this species are difficult to determine. The major predators in the WP area are inferred to be the crabs, *Cancer gracilis* and *C. productus*. Both crabs were common and have been shown to eat other, larger, turrid gastropods in the same area (SHIMEK, 1982, 1983). Nonetheless, no direct evidence of this predation was encountered. *Kurtziella* is a small snail with a relatively fragile shell, and attacks by these large crabs probably result in the complete destruction of the shell. Unlike *Ophiidermella* and *Oenopota* species, *Kurtziella* does not show any significant tendency to bury; this may result in substantial mortality when the predatory crabs are common. The relative rarity of the species at WP during and after the summer population peak of the crabs is likely the result of predation. The smaller mean length of individuals in the WP population, compared to the FHL population may result from some size-selective predation by the crabs on larger snails. Immigration from deeper habitats where the crabs are less common is probably responsible for the recovery of the population.

Mortality effects at FHL are unknown. During the course of study, over 100 turrid shells were recovered with hermit crabs in them. These shells proved useful in determining some of the causes of mortality of some of the other turrids in the region (SHIMEK, 1982, 1983), but no *Kurtziella* shells were recovered. This may be indirect evidence of predation by crushing predators like crabs, which can sometimes be found in the FHL habitat. Some fishes may also eat the snails. Except for *Luidia foliolata* Grube, 1866, predatory asteroids are uncommon in the area.

In both populations, the snails appear to have a defined maximum size of about 15 mm. Growth may cease or slow as the animals approach this size, thus making measurement of growth rates difficult. There is no indication of semelparity in this species. After spawning, the females appear healthy, and all were marked and returned to their habitat.

In conclusion, *Kurtziella* requires sandy or sandy-mud habitats, and overall is a dietary generalist, although it may specialize in some populations. Thus, the hypothesis that *Kurtziella plumbea* is a "Jack-of-all-trades" for both diet and habitat is rejected. It is likely that suitable sandy or sandy-mud habitats are widespread on the Pacific coast of North America; this turrid should be expected in many of them. That this species will be rarely found in rocky or shell-fragment areas is also predicted.

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Editor's note: After the issue had gone to press, we were informed that the paper referred to as "Shimek, 1982" throughout the present article was published in 1983.